

## RESEARCH ARTICLE

# Sources of Tooth Wear Variation Early in Life Among Known-Aged Wild Ring-Tailed Lemurs (*Lemur catta*) at the Bezà Mahafaly Special Reserve, Madagascar

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Ring-tailed lemurs (*Lemur catta*) at the Bezà Mahafaly Special Reserve (BMSR), Madagascar display a high frequency of individuals with notable and sometimes extreme tooth wear. Adult lemurs display a range of tooth wear even among individuals of the same age, but we do not know at what age this variation first appears. This study's goal was to determine whether wear variation occurs in younger wild lemurs. Based on the decade-long study of ring-tailed lemur feeding and dental ecology at BMSR, we hypothesized that younger, natal lemurs (under 5 years of age), would display variation in their degree of tooth wear that would correspond to microhabitat differences, given differences in food availability in different troops' home ranges. We also hypothesized that wear would differ between sexes at this young age, given differences in feeding between males and females in this population. Hypotheses were tested using dental topographic analyses using dental impressions collected from known-aged lemurs across 10 years at BMSR. Results illustrate significant differences in wear-related tooth topography (i.e., relief and slope, presented here as "occlusal lift") for microhabitat, sex and troop affiliation among lemurs under 5 years of age in this population. Although, all lemurs in this population consume mechanically challenging tamarind fruit, those in more disturbed habitats eat additional introduced foods, some of which are also mechanically challenging. Thus, dietary variation is the likely cause of variation in tooth wear. The wear variation we show at a young age suggests caution when assigning age based on tooth wear in living and fossil primates. These wear-related tooth shape changes early in life, which reflects sex, habitat variation and levels of anthropogenic disturbance, may potentially impact reproductive fitness later in life. *Am. J. Primatol.* 76:1037–1048, 2014. © 2014 Wiley Periodicals, Inc.

**Key words:** dental topography; life history; dental ecology; sex; habitat

## INTRODUCTION

Dental morphology reflects important foods in a species' diet, with their shape and structure varying to allow efficient fracture of foods with given material properties [e.g., Lucas, 2004; Ungar, 2010]. However, tooth wear can affect functionality, with potential influences on survival, health, and life history [Cuzzo & Sauter, 2006; King et al., 2005; Lanyon & Sanson, 1986; Logan & Sanson, 2002a,b; Veiberg et al., 2007]. Thus, we would expect that natural selection should select for teeth with properties that resist wear and/or "sculpt" in a manner that maintains functional efficiency [e.g., Lucas, 2004; Teaford, 1983; Ungar, 2010; Ungar & M'Kirera, 2003]. To date, there have been few longitudinal studies of tooth wear controlling for age in wild non-human primates [see review in Morse et al., 2013]. Repeated captures of 14 wild mantled howling monkeys (*Alouatta*

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*palliated*) found no differences in molar gross wear by microhabitat [Dennis et al., 2004]. On the other hand, differences in the rate and onset of tooth wear are reported for wild Ethiopian and Tanzanian baboons living in different localities, perhaps related to ground cover, sociality, or seasonal food availability [Phillips-Conroy et al., 2001]. More recent work on Kenya's Amboseli baboons [Galbany et al., 2011] has demonstrated that, in addition to age, individual feeding behaviors do correspond to differences in tooth wear. Despite these examples, our knowledge of how teeth "sculpt" in living primates across their lives remains quite limited.

Dental morphology generally reflects long-term adaptation to diet, reflected, for example, in the hypothesis that use of certain fallback foods leads to specific dietary characteristics, such as enamel thickness [e.g., Pampush et al., 2013; Vogel et al., 2008]. Numerous studies have shown that primate folivores and insectivores have longer molar shearing crests than do closely related frugivores [Rosenberger & Kinzey, 1976; Seligsohn & Szalay, 1978]. The standard measure of shear potential has been Kay's [1975] shearing quotient (SQ), involving regression of the summed length of molar shearing crests and against the mesiodistal length of a tooth. Indeed, folivorous primates tend to have higher SQ values (residuals from the regression line) than frugivores; and among frugivores, hard-object feeders have the lowest SQ values [Kay & Covert, 1984; Meldrum & Kay, 1997]. This approach is valuable for characterizing dental function in primates, though it can be problematic for studies of worn teeth as landmarks used to measure SQ (e.g., cusp tips) are obliterated with wear.

As a means of avoiding this problem, functional aspects of worn teeth can also be considered in whole-surface characterizations, such as dental topographic analysis (DTA) [e.g., Ungar & Williamson, 2000; Zuccotti et al., 1998]. DTA models the occlusal surface of molars with tools designed to analyze geographical landscapes. First, three-dimensional (3D) point clouds of  $x$ ,  $y$ , and  $z$  coordinates are generated for molar surfaces by laser scanning. Surfaces are interpolated by inverse-distance weighting using Geographic Information System (GIS) software to create a digital elevation model (DEM). The DEM allows calculation of mean slope (i.e., the relative difference between adjacent points expressed in degrees) and angularity (the average rate of change in slope between adjacent points) of the occlusal table. The occlusal table is defined by cropping a molar surface to include only the area above the lowest point on the occlusal basin. Following Dennis et al. [2004], this cropping is done for each tooth, which is oriented such that the maximum occlusal surface is facing normal to the plane of the scanning field. This process facilitates characterization of dental topography of even heavily worn specimens

as it minimizes reliance on landmarks that can be obliterated by wear. The software also uses the 3D software to fit triangles to adjacent cells in the DEM to create a triangulated irregular network (TIN). The summed area of these triangles provides a measure of the surface area of the occlusal table. The ratio of surface area to the underlying planimetric area gives a measure of topographic relief.

DTA has largely affirmed results from SQ studies. Highly-crested folivorous primates have correspondingly high topographic relief and average surface slope, and those with shorter crests have low topographic relief and slope [Bunn & Ungar, 2009; M'Kirera & Ungar, 2003]. Folivorous primates also tend to have more jagged, angular occlusal surfaces with higher occlusal surface angularity than frugivorous species. Interestingly, Ungar and M'Kirera [2003] found that not only did angularity differences between chimpanzees and gorillas hold at given stages of gross dental wear, but that these values did not vary within species for differently worn molars [but see Klukkert et al., 2012]. Mantled howling monkey molar angularity does not appear to vary between individuals living in riparian and non-riparian forest microhabitats, though this value does drop with extreme wear [Dennis et al., 2004]. Bunn and Ungar [2009] similarly found that angularity in Old World monkeys only drops with extreme wear, though differences in angularity between species were evident. The drop in angularity with extreme wear may reflect dental senescence, and with it a marked drop in functional efficiency of the tooth for chewing [Ungar, 2005]. The potential impact of dental senescence on reproductive success has been suggested by King and colleagues [2005], who documented a correlation between high mortality rates in infants of lemur mothers (*Propithecus edwardsi*) with "senescent" teeth, specifically during periods of environmental stress, that is, reduced rainfall. However, direct assessment of the effects of advanced tooth wear on nutrient intake, and its potential impact on life history variables such as infant survival, is needed [Millette et al., 2012]. In addition, an operational understanding of what senescence actually means in terms of dental function remains elusive. We still have much to learn about how occlusal topography changes with tooth wear, and its broader implications (i.e., senescence). Can we assume that individuals within a species, and even within a population have similar dental topography for a given age if they vary in diet? Moreover, to what degree does molar angularity remain constant within a species, and can change in this attribute be used consistently to identify senescence? In addition, at what age might differences in angularity and overall occlusal topography, appear within a population? If differences in "wear" as reflected in variation in occlusal topography occur early in life, what are the potential life history

ramifications later in life? We investigate these issues using a dental ecology approach [Cuozzo & Sauther, 2012] through a longitudinal examination of molar wear (as illustrated through DTA) of wild ring-tailed lemurs (*Lemur catta*) at the Bezà Mahafaly Special Reserve (BMSR) in southern Madagascar.

BMSR ring-tailed lemurs have been studied intensively for more than two decades [e.g., Cuozzo et al., 2010; Sauther, 1992, 1994; Sauther & Cuozzo, 2009; Sussman, 1991; Sussman et al., 2012]. These primates are dietary generalists, consuming fruit, flowers, leaves, and at times insects, depending on availability [Sauther, 1992, 1998]. All members of a troop generally feed together, but foods consumed can vary between sexes, and even by rank within sexes, and food resource availability is extremely seasonal [Cuozzo et al., 2010; Sauther, 1992, 1998, 2002; Sauther & Cuozzo, 2009]. Within the BMSR riverine gallery forest, numerous ring-tailed lemur troops (consisting of up to 25 individuals) subsist in different microhabitats (which we refer to here as *Reserve*, *Marginal*, and *Camp*), and exploit foods as they become available as reflected by plant phenology [e.g., Gemmill & Gould, 2008; Sauther, 1994, 1998]. Within the fenced 80 ha protected “reserve” (“Parcel 1”), the habitat grades from a riparian forest at the eastern boundary of the Sakamena River, to a mixed dry, xerophytic/scrub forest toward the western boundary [Gemmill & Gould, 2008] (Fig. 1). Outside the reserve, in the “marginal” microhabitat, the forest is degraded by anthropogenic effects, including livestock use, and has reduced ground/canopy cover and a subsequent reduction of many preferred foods used within the protected forest [Cuozzo & Sauther, 2004; Sauther et al., 2006; Sauther & Cuozzo, 2009; Sussman & Rakotozafy, 1994]. Some lemur troop’s home ranges also include the BMSR “camp,” which borders the reserve and marginal microhabitats, and provides access to anthropogenic resources [Fish et al., 2007; Gemmill & Gould, 2008; Sauther et al., 2006].

At BMSR, many (but not all [Cuozzo et al., 2010]) ring-tailed lemurs exhibit exceptionally high frequencies of severe tooth wear and antemortem tooth loss, which are more rapid and dramatic than reported for any other primate population [Cuozzo & Sauther, 2004, 2006, 2012; Millette et al., 2009; Sauther et al., 2002]. We have suggested in these previous publications that this pattern of severe wear is due, at least in part, to consumption of the mechanically challenging tamarind fruit (*Tamarindus indica*). Tamarind fruit is the hardest and toughest of all regularly consumed foods at BMSR [Yamashita et al., 2012]. As a result of these properties, tamarind fruit requires numerous bites to open the fruit, thus resulting in frequent and repeated contact between the teeth and challenging exocarp of the fruit [Yamashita et al., 2012]. In addition, our ongoing work indicates that tamarind

fruit at BMSR is grit-laden, thus increasing tamarind’s potential to cause tooth wear in these lemurs (Cuozzo et al., unpublished data). Because tamarind fruit is ubiquitous year round in each microhabitat [Sussman & Rakotozafy, 1994] it represents an important fallback food, exploited especially during the dry season [Sauther & Cuozzo, 2009]. However, outside of the protected “reserve,” human induced alteration has resulted in virtually no ground cover or lower canopy, leaving mature tamarind trees as a perpetual primary resource [Whitelaw, 2010; Whitelaw et al., 2005], resulting in females outside the protected reserve (the human-altered *marginal* microhabitat) exhibiting higher frequencies of severe tooth wear and antemortem tooth loss than those females living primarily within the “reserve” microhabitat [Cuozzo & Sauther, 2006; Sauther et al., 1999; Sauther & Cuozzo, 2009]. In addition to microhabitat, we would also expect differences in tooth wear between males and females, whose diets may differ because of this species’ female dominance, with females having priority of access to all foods [Sauther, 1992; Sauther & Sussman, 1993]. There may also be differences within sexes, as higher-ranking females within matriline frequently consume higher quality foods [Sauther, 1992; Sauther et al., 2002].

As a result of reproductive synchrony [e.g., Pereira, 1991; Sauther, 1991; Sauther et al., 1999] ring-tailed lemurs occur as discrete age cohorts. All members of an age cohort in the present study were born within weeks of each other during late September early October prior to the beginning of the wet season, which occurs October to May at BMSR. Additionally, the data we present here are controlled by age and microhabitat, restricted to 2–4 years old individuals that have not yet left their natal troops, thereby eliminating the effect of migration and the exploitation of multiple habitats. All 2-year old lemurs in the study sample displayed fully-erupted and functional molars, with most also possessing the full suite of adult premolars.

Ring-tailed lemurs at BMSR subsist in a variety of microhabitats (each with differing food type availabilities and abundances) and exhibit variable foraging based on sex and troop affiliation, as well as social rank [Cuozzo et al., 2010; Sauther, 1998; Sauther et al., 1999, 2002]. All troops in this population rely on hard, tough tamarind fruit as a fallback food (*Tamarindus indica*) [e.g., Cuozzo & Sauther, 2006; O’Mara, 2012; Sauther, 1992, 1998; Sauther & Cuozzo, 2009; Yamashita, 2002; Yamashita et al., 2012]. However, these lemurs also utilize other mechanically challenging and/or introduced foods, the availability of which varies by microhabitat and by the degree of anthropogenic impact. Among these foods, introduced *Aloe divaricate* is one of the five toughest foods eaten by the BMSR lemurs, a food which, similar to tamarind fruit, requires numerous

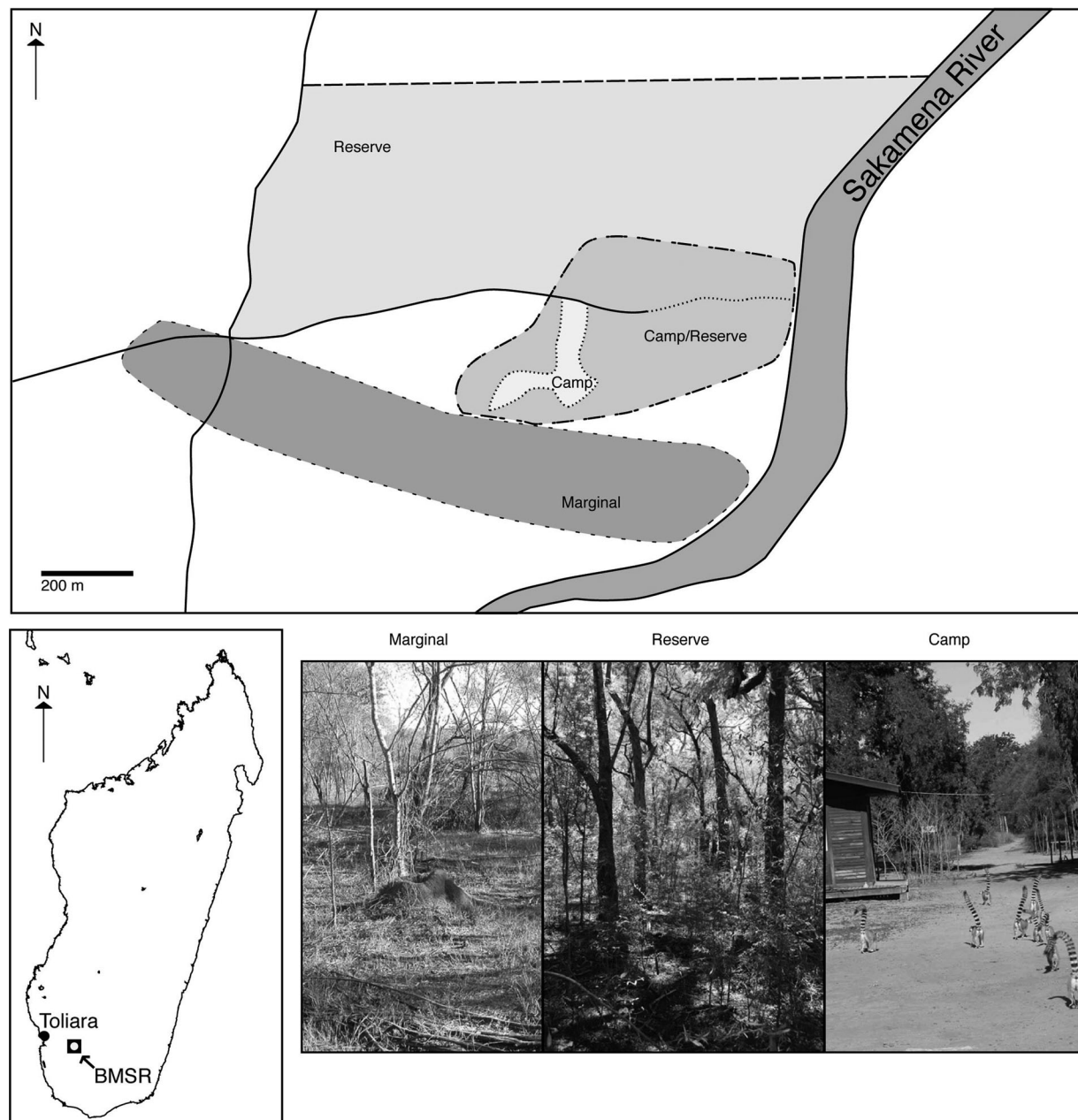


Fig. 1. Map of Beza Mahafaly Special Reserve depicting microhabitat borders and pictures of the marginal, reserve, and camp microhabitats.

bites to process [Yamashita et al., 2012]. Outside of the reserve boundaries, human actions have greatly reduced the forest understory forcing lemurs to continually emphasize specific foods such as tamarind or introduced foods such as aloe leaves [e.g., Sauther & Cuozzo, 2009; Yamashita et al., 2012]. This primate population is thus well suited to the study of whether anthropogenic factors, sex, and/or microhabitat variation affect dental topography over time, and thus potential dental function.

The goal of our study is to explore at what age variation in tooth wear occurs in this primate

population. Our previous work shows that variation is present in older, adult lemurs. Thus, we hypothesize that such wear variation will be present in younger lemurs, under 5 years of age (Hypothesis 1). In addition, given sex and microhabitat differences in feeding, we hypothesize that variation in tooth topography (relief and slope) will also vary between sexes and across microhabitats, even at this young age (Hypothesis 2). Furthermore, as previous studies suggest that angularity in moderately worn molars is constant in a species, we hypothesize that angularity will not be affected by microhabitat, sex, and/or troop,

at least until the latest stages of wear (Hypothesis 3). In addition to helping understand relationships of dental topography to wear, these data will inform the tenability of assuming species-specific wear rates when reconstructing ages of fossil primates based on worn teeth.

## METHODS

All methods and materials described herein received approval by and followed standard animal handling guidelines and protocols of the Institutional Animal Care and Use Committees of the University of North Dakota and/or the University of Colorado (most recent—University of North Dakota, IACUC #0802-2, approved 04/03/08). Data collection in Madagascar was conducted with approval by MNP (Madagascar National Parks, formerly known as ANGAP [Association Nationale pour la Gestion des Aires Protégées]), the body governing research in Madagascar's protected areas, and with CITES approval (05US040035/9). Additionally, all research was conducted in compliance with the American Society of Primatologists' Principles for the Ethical Treatment of non-Human Primates.

### Experimental Design

Our study examines potential effects of microhabitat (reserve, marginal, camp/reserve; see Fig. 1), sex, troop and age on ring-tailed lemur molar topography as measured by mean slope, topographic relief, and mean angularity. First and second lower molars were examined separately, as previous research has suggested these may have independent wear rates and changes in dental topography in at least some primates [Bunn & Ungar, 2009]. Our analyses are based on multiple captures of 32 individuals, with each lemur captured 3 consecutive years, at 2, 3, and 4 years of age, for a total of 96 captures. Of these 32 lemurs, 17 are female and 15 are male. Lemurs sampled come from ten different troops, each the focus of long-term study since 2003. Two troops with sufficient samples for group comparison (orange troop,  $N=7$  and blue troop,  $N=5$ ) are highlighted. These two troops inhabit adjacent areas, with both frequently found in areas south and/or west of the protected reserve, although, orange most often sleeps within the area known as Parcel 1 (Sauther and Cuzzo, unpublished data), along the southern reserve's southern edge. Orange troop also exploits the research camp, while blue troop has the largest range of all BMSR troops studied, sometimes exploiting anthropogenically altered habitats along the ephemeral Sakamena River, using crops and other introduced foods in addition to the endemic foods consumed by all BMSR troops.

### Lemur Sampling Protocol

Data presented herein result from captures of living lemurs across eight field seasons (2003–2010)

at the Beza Mahafaly Special Reserve in Madagascar (23°30'S, 44°40'E). Dental impressions were collected by FPC and MLS. Veterinarians and veterinary students supervised 300+ overall captures between 2003 and 2010 [Cuzzo et al., 2010; Larsen et al., 2011a,b]. Lemurs were captured using either a Telinject<sup>®</sup> (Telinject USA, Inc., Agua Dulce, CA) or Dan-Inject<sup>®</sup> blow dart system (Dan-Inject, North America, Fort Collins, CO) with ketamine hydrochloride (Ketaset, Fort Dodge Animal Health, Fort Dodge, IA), ketamine and diazepam (Valium, Roche, Inc., France), Telazol<sup>®</sup> (Fort Dodge Laboratories) or various combinations of these drugs as anesthesia, as part of the assessment of varied protocols [Larsen et al., 2011a,b; Sapolsky & Share, 1998]. Initial capture of BMSR ring-tailed lemurs occurs as "subadults," late in their 2nd year of age (approximately 20–22 months of age, depending on capture date, which ranges from early June through early August each year). Age is determined through a combination of characteristics, including dental development (i.e., canine eruption), body mass, somatic information, and long-term census data for the population when available. All individuals described in this study were first captured as described above, late in their 2nd year of age and are thus of known age. Given reproductive synchrony, these lemurs are members of a yearly cohort, with all lemurs being born within 4–6 weeks of each other. Upon initial capture, numbered collars were placed on each lemur for long-term identification and study [e.g., Cuzzo et al., 2010]. Dental impressions were collected using customized impression trays and President Plus Jet Regular Body polyvinylsiloxane impression material (Coltene<sup>®</sup>-Whaledent, Mawah, NJ) [Cuzzo et al., 2010]. Unlike studies of dental microwear, teeth were not cleaned prior to making dental impressions. For this study only individuals ages 2–4 years were compared, as this age range predates usual migration from natal troops at BMSR, which, for males, occurs primarily between 4 and 5 years of age (Sauther and Cuzzo, unpublished data). All individuals in this study were thus still in their natal troops, allowing us to compare microhabitats while controlling for the potential effects of migration. We note the control of this important variable, as it is especially relevant for understanding its potential impact in the analysis of fossil specimens.

### Dental Topography

These methods follow protocols detailed elsewhere [Bunn & Ungar, 2009; Dennis et al., 2004]. All dental topographic analyses were conducted by BRH and PSU. High-resolution replicas were made from impressions using Epo-Tek<sup>®</sup> 301 and pigment (Epoxy Technologies, Billerica, MA), and were then coated with a thin layer of Magnaflex<sup>™</sup> SKD-52

Developer (Illinois Tool Works, Glenview, IL) to mitigate replica translucency. Specimens were then scanned using a XSM multi-sensor scanning system (Xystum Corp., Turino, Italy) with an integrated OTM3 laser head (Dr. Wolf and Beck GmbH, Wangen, Germany). Specimens were scanned such that maximum occlusal surface area was normal to the stage following convention. The laser scanner created three-dimensional point clouds by collecting  $z$  elevations at an interval of 25  $\mu\text{m}$  along  $x$  and  $y$  axes. The point clouds were processed as ASCII files in Digiline<sup>TM</sup> software (Xystum Corp.) and imported as tables in ArcView<sup>TM</sup> 3.2 geographic information systems software with the Spatial Analyst and 3D Analyst Extensions (ESRI Corp., Redlands, CA). Slope and angularity were calculated from resultant DEMs and topographic relief from TINs.

### Statistical Analyses

Statistics and plots were generated using JMP<sup>®</sup> 8.0.2 (SAS Institute, Inc., 2009) and R 2.12.1 (R Foundation for Statistical Computing, 2010) with the RStudio 0.91.23 (RStudio, 2011) GUI. First, data were transformed to conform to a normal distribution for statistical analyses. This was done to balance distribution requirements for parametric statistics with the need for statistical power given sample sizes and “noise” introduced by individual variation. Such transformations are a common and critical technique to help data to meet the assumptions of ANOVA tests, as employed herein [Sokal & Rohlf, 1995]. Angularity data were transformed using a tangent transformation, which works especially well for highly skewed datasets, such as surface angularity. Because topographic relief and mean slope are likely correlated, the two were reduced into a single variable, called here *occlusal lift*. Following Quinn and Keough [2002], occlusal lift is the first component of a principal components analysis (PCA) calculated with covariances. This variable describes change in elevation across the surface of the tooth, one of the most important attributes of dental form associated with function and wear. Occlusal lift data were

normalized using an exponential transform and shift, using the formula  $((M_1 \text{ PCA} + 20)^2)/100$ .

Statistical analyses employed a two-tailed Repeated Measures Analysis of Variance (RM-ANOVA) design. This approach is commonly used with repeated measures of the same individuals over time, as in this case. The RM-ANOVA partitions variation within individuals by age in the same way as does a randomized blocks design or paired comparisons test [Quinn & Keough, 2002]. In other words, the test can detect true dental wear over time and between treatments by portioning out repeated sample variation. More specifically, our test procedure followed the procedure outlined in Looney and Stanley [1989] and Quinn and Keough [2002]. RM-ANOVAs were run for each variable, with an experiment-wise error rate (Bonferroni procedure) used to reduce probability of type I error (incorrect rejection of a true null hypothesis) given multiple tests (Table I). This table represents the adjustments made for experiment-wise hypothesis testing bias, to control for higher error rates. In other words, we made it harder for our hypotheses to be significant. This table also shows the  $P$  value of the test, versus the adjusted alpha value. Separate tests for angularity and occlusal left were run for  $M_1$  and  $M_2$  for microhabitat (marginal, reserve, and camp/reserve), sex (male and females), and troop (blue and orange). All statistical data presented herein come from the RM-ANOVA tests described above, and were conducted by BRH. A  $P$  value for all tests equal to or less than 0.05 was considered to be statistically significant.

## RESULTS

### Microhabitat

Results indicate a significant effect of microhabitat on  $M_1$  occlusal lift but not so for  $M_2$  (Table II). Neither  $M_1$  nor  $M_2$  shows a significant effect of microhabitat on angularity. Table III shows that, specifically, marginal microhabitat  $M_1$  occlusal lift (Mean =  $4.43 \pm 0.34$ ,  $F = 9.312$ ,  $DF = 1$ ,  $P = 0.004$ ,  $n = 10$ ) is significantly lower than camp/reserve and reserve values (Mean =  $4.96 \pm 0.22$ ,  $F = 9.312$ ,

**TABLE I. Sequential Bonferroni Tests and Results: Adjustments Made for Experiment-Wise Hypothesis Testing Bias**

Test	Equation <sup>a,b</sup>	Adjusted alpha	$P$ value	$P < \alpha$ ?
$M_1$ Habitat	$a/c$	0.025	0.013332	Yes
$M_2$ Habitat	$a/(c-1)$	0.05	0.336888	No
$M_1$ Sex	$a/c$	0.025	0.024649	Yes
$M_2$ Sex	$a/(c-1)$	0.05	0.521747	No
$M_1$ Troop	$a/c$	0.025	0.000361	Yes
$M_2$ Troop	$a/(c-1)$	0.05	0.000445	Yes

<sup>a</sup>Alpha ( $\alpha$ ) = 0.05.

<sup>b</sup>No. of tests ( $c$ ) = 2.

TABLE II. RM ANOVA Comparisons for Angularity and Occlusal Lift

	Angularity <sup>a,b,c</sup>					Occlusal Lift <sup>a,b,c</sup>				
	DF	MS	F	P	n	DF	MS	F	P	n
Microhabitat										
M <sub>1</sub>	2	0.062	0.973	0.385	28	2	2.630	4.713	<b>0.013</b>	28
M <sub>2</sub>	2	0.083	2.466	0.095	28	2	0.649	1.112	0.337	28
Sex										
M <sub>1</sub>	1	0.228	2.885	0.094	32	1	0.000	0.415	0.552	32
M <sub>2</sub>	1	0.082	2.827	0.098	32	1	0.003	5.312	<b>0.024</b>	32
Troop										
M <sub>1</sub>	1	0.235	2.339	0.142	12	1	0.006	18.364	< <b>0.001</b>	32
M <sub>2</sub>	1	0.000	0.003	0.958	12	1	0.006	17.605	< <b>0.001</b>	32

<sup>a</sup>Bold values indicate significant  $P \leq 0.05$  values.

<sup>b</sup>M<sub>1</sub>, first mandibular molar; M<sub>2</sub>, second mandibular molar.

<sup>c</sup>DF, degrees of freedom; MS, mean square (=variance); F, F-ratio.

DF = 1,  $P = 0.004$ ,  $n = 18$ ). No such difference is seen for M<sub>2</sub> occlusal between marginal microhabitat and camp/camp reserve. No significant differences are seen in occlusal lift between the camp and camp/reserve microhabitats for occlusal lift.

### Sex

Data on the effect of sex on occlusal lift and molar angularity (Table II) indicate no differences between males and females for M<sub>1</sub> occlusal lift. M<sub>2</sub> occlusal lift did vary significantly between the sexes (Females: Mean =  $2.05 \pm 0.01$ ,  $F = 5.312$ , DF = 1,  $P = 0.024$ ,  $n = 17$ ; Males: Mean =  $1.99 \pm 0.01$ ,  $F = 5.312$ , DF = 1,  $P = 0.024$ ,  $n = 15$ ) Angularity for M<sub>1</sub> and M<sub>2</sub> did not differ by sex (Table II).

### Troop

Although, dental data from individuals belonging to ten different troops at BMSR are included in our study, only two troops (orange and blue troops) had sufficient numbers of individuals to allow robust comparisons between troops. RM-ANOVA tests indicate that blue and orange troops differed significantly in M<sub>1</sub> occlusal lift (Table II). Orange lemurs (Mean =  $2.01 \pm 0.01$ ,  $F = 18.364$ , DF = 1,  $P = <0.001$ ,  $n = 7$ ) have higher M<sub>1</sub> occlusal lift values than lemurs of Blue troop (Mean =  $1.98655 \pm 0.01$ ,  $F = 18.364$ , DF = 1,  $P = <0.001$ ,  $n = 5$ ). As with M<sub>1</sub>, blue and

orange troops differed significantly in M<sub>2</sub> occlusal lift: blue troop (Mean =  $1.99549 \pm 0.01$ ,  $F = 17.605$ , DF = 1,  $P = <0.001$ ,  $n = 5$ ), orange troop (Mean =  $2.02 \pm 0.01$ ,  $F = 17.605$ , DF = 1,  $P = <0.001$ ,  $n = 7$ ). Similar to habitat and age, angularity was again not significant for any main effects for either M<sub>1</sub> or M<sub>2</sub> (Table II).

### DISCUSSION

Our primary goal in this study was to assess whether tooth wear—represented here by the dental topographic variables angularity, relief, and slope—varies in younger ring-tailed lemurs at the Beza Mahafaly Special Reserve, Madagascar. The results presented here demonstrate that same-aged, young lemurs from a single population do vary in occlusal lift, a measure that combines relief and slope (see Methods section). Thus, Hypothesis 1, that wear variation will be present in younger lemurs, under 5 years of age, is supported. This variation is seen across microhabitats and troops and between males and females. We also predicted that tooth topography (relief and slope) would also vary between sexes and across microhabitats (Hypothesis 2). Occlusal lift values do differ between M<sub>1</sub> and M<sub>2</sub> according to microhabitat, sex, and/or troop, thus Hypothesis 2 is supported. However, no such differences were observed for angularity. Therefore, Hypothesis 3 that

TABLE III. RM-ANOVA Comparisons for Occlusal Lift Between Specific Microhabitats

	M <sub>1</sub> <sup>a,b,c</sup>					M <sub>2</sub> <sup>a,b,c</sup>				
	DF	MS	F	P	n	DF	MS	F	P	n
Marginal versus camp/reserve & reserve	1	5.198	9.312	<b>0.004</b>	28	1	0.034	0.058	0.810	28
Reserve versus camp/reserve	1	0.102	0.183	0.671	18	1	1.250	2.143	0.150	18

<sup>a</sup>Bold values indicate significant  $P \leq 0.05$  values.

<sup>b</sup>M<sub>1</sub>, first mandibular molar; M<sub>2</sub>, second mandibular molar.

<sup>c</sup>DF, degrees of freedom; MS, mean square (=variance); F, F-ratio.



angularity will not be affected by microhabitat, sex, and/or troop, is supported. These results from younger-aged ring-tailed lemurs correspond with most previous studies on apes and monkeys, in which species' molar teeth wear in such a way that mean slope and relief decrease with wear, but angularity (i.e., surface jaggedness) does not vary significantly with wear, at least among younger individuals [Bunn & Ungar, 2009; Dennis et al., 2004; M'Kirera & Ungar, 2003; Ungar & M'Kirera, 2003; but see also Klukkert et al., 2012]. What may explain the patterns of gross tooth wear variation we describe here in this lemur population?

We expected that there would be differences in tooth wear across microhabitats, and thus between troops inhabiting these different landscapes. Feeding data from over 20 years of study show that tamarind fruit, and its challenging mechanical properties, is used by all BMSR troops [e.g., Cuozzo & Sauter, 2004, 2006, 2012; O'Mara, 2012; Sauter, 1992, 1998; Sauter & Cuozzo, 2009; Whitelaw, 2005; Yamashita, 2002]. However, there is feeding variation in the reserve and in the surrounding areas inhabited by the BMSR lemurs, based on the varied distribution of specific plants, including those resulting from anthropogenic change [e.g., Gemmill & Gould, 2008; Sauter & Cuozzo, 2009]. Here anthropogenic change may have important effects on primate molar shape, with individuals living in marginal habitats showing reduced  $M_1$  occlusal lift at every age (Tables II and III). Figure 2 illustrates this as well, showing a

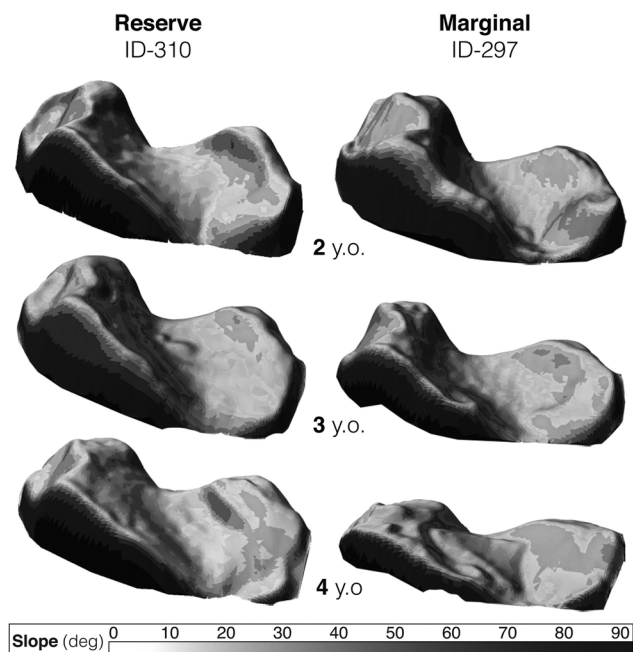


Fig. 2. 3D, shaded, slope topographic models of  $M_1$ s of two ring-tailed lemurs sampled yearly from age 2 to 4. Notice the exacerbated wear in the marginal habitat lemur (Blue 297, female) at age four compared to a reserve habitat lemur (Teal 310, female).

dramatic visual difference in overall  $M_1$  occlusal wear in two same-aged, female ring-tailed lemurs. Teal 310 lives in the center of the protected reserve while Blue 297 lives within a marginal habitat whose troop ranges as far as several kilometers each day, mostly through areas affected by intense human activity, including degraded forest and cropland. Teal troop maintains a much smaller daily home range, and has never been seen to move outside of the protected reserve. The diet of Blue troop thus differs from Teal in that blue troop uses a number of introduced foods not found in the reserve, such as bageda leaves (*Ipomoea batatas*, the local cultivated sweet potato) and several species of aloe (*Aloe divaricate* and *Aloe vahombe*)—all food resources not consumed by Teal troop [Sauter and Cuozzo, 2009; Whitelaw, 2010; O'Mara, 2012]. Among 20 foods for which food properties have been analyzed at BMSR, aloe is amongst the toughest consumed [Yamashita et al., 2012]. It is also the largest food consumed, requiring a high number of bites per bout, similar to that of tamarind fruit [Yamashita et al., 2012; see Fig. 3]. Blue troop is thus using additional foods (beyond those used by all troops, such as tamarind fruit) with challenging mechanical properties compared to Teal troop. Such differential food use likely contributes to the differences in wear patterns between individuals in marginal versus reserve habitats, exemplified by the visual differences seen in these two same-aged females.

The use of introduced foods in anthropogenic habitats may also explain why orange troop lemurs have less tooth wear (i.e., greater occlusal lift in both  $M_1$  and  $M_2$ ) than those of blue troop. Blue troop frequently uses human crops and feeds in areas with notable anthropogenic disturbance, in contrast to orange troop. A key example is the use of the leaves of bageda (the local sweet potato), as noted above. This crop is grown in the alluvial plains of the Sakamena River bordering BMSR. As a result, these leaves may



Fig. 3. Two-year old, female, ring-tailed lemur feeding on aloe at Beza Mahafaly Special Reserve.



be grit laden, and exogenous grit has been suggested, and more recently demonstrated, to be a source of enamel wear in primates and other mammals [e.g., Galbany et al., 2011; Kay & Covert, 1983; Lucas et al., 2013; Morse et al., 2013; Romero et al., 2012; Ungar et al., 1995; Williams & Kay, 2001] (Cuozzo et al., unpublished data) and thus may exacerbate the pattern of wear already due to tamarind fruit consumption. As noted above, Blue troop also feeds on additional challenging foods such as aloe. Orange troop has been using camp resources for over 20 years. Most of these anthropogenic foods are easily processed and include cooked bageda (e.g., local sweet potatoes, taken from the camp's cooking area), a variety of melons, carrots, mangos, oranges, and pineapple [Sauther et al., 2006]. Having access to such resources likely provides a less abrasive or less mechanically challenging nutritional buffer, especially during the dry season, and may in part explain the higher occlusal lift seen in Orange troop as compared to Blue troop.

In these younger-aged lemurs (2–4 years of age) we may also be seeing the early effects of sex differences in feeding, as reflected in the difference between male and female values, where males show significantly lower occlusal lift values than females for  $M_2$  (although, not for  $M_1$ ) (Table II). This pattern of greater wear in males compared to females may relate to female feeding priority, with males exploiting challenging fallback tamarind fruit more frequently [Gemmill and Gould, 2008], or possibly using other lower quality foods [Sauther et al., 2002]. But, why would there be no difference in occlusal lift in  $M_1$ ? As  $M_1$  erupts first, at roughly the 4th month of age, corresponding to the onset of weaning, the lack of a difference in  $M_1$  occlusal lift between males and females may be a result of the signal between the sexes being lost due to wear, given that by the 4th year  $M_1$ s can be notably worn (see Fig. 2). As  $M_2$  erupts later, at approximately the 8th month, the difference in occlusal lift between males and females is more readily detectable in these 2–4 year old lemurs and might be a more accurate reflection of sex differences in feeding at this young age, which remain throughout life among ring-tailed lemurs, and which is notable especially during lactation [O'Mara, 2012; Sauther, 1991, 1992]. Indeed, among those lemurs between 1 and 2 years of age studied in 2009–2010, there is already a significant sex difference in time spent feeding on tamarind fruit with males feeding more than females [O'Mara, 2012].

Our results illustrate that tooth wear, as reflected in tooth shape, can vary within a single population of a species, depending on microhabitat and sex of the individuals, which supports earlier conclusions from a smaller sample that gross tooth wear can vary among same-aged individuals in a given population [Cuozzo et al., 2010]. It is also important to note that our new data come from

known-aged lemurs, all 2–4 years old. At Beza Mahafaly, this age range represents developmentally, behaviorally, and reproductively young individuals. In this population it is only in or after their 4th year of life that male lemurs generally migrate from their natal troops, that females successfully give birth (females can give birth earlier, but these infants do not tend to survive), and that both sexes achieve full biological maturity in terms of somatic and dental growth and development (Sauther and Cuozzo, unpublished data). Thus, our new data indicate that differences in occlusal lift begin prior to major “life history” changes; and, they strongly suggest the importance of microhabitat and sex on wear-related tooth shape in a single primate population. We expect trend differences to be even more dramatic in older individuals, given the ecological complexity of diet in these primates.

Our work illustrates that food choice and/or availability across sexes and troops, as well as anthropogenic impact, can have implications for how primate teeth wear early in life. This can have broad implications on life history parameters and variables such as reproductive success. King and colleagues [2005] have argued that tooth wear in older female lemurs (*Propithecus edwardsi*) impacts infant mortality. Specifically, they argue that during periods of resource stress, such as reduced rainfall, worn teeth in older female sifaka correlates with increased infant mortality, suggesting an inability to adequately process food, thereby leading to reduced infant survival. What is not known is when this wear begins to occur, and how this may set the stage for such eventual life history impacts. Our data suggest that wear-related changes in tooth shape occur early in life for ring-tailed lemurs at this locality, with variation becoming significant between troops, sexes and microhabitat as early as 4 years of age. Thus, when contemplating the impact of tooth wear on life history, our data indicate that the “stage may be set” early in life, as wear-related variation in tooth shape is apparent in this population even before reaching sexual maturity. How this variation in our current sample of young lemurs impacts future life history variables/parameters, such as life-span or reproductive success, will be documented as we follow these lemurs throughout their lives.

As a final note, this study provides a cautionary tale for age assessment based on gross dental wear in living and fossil species. Tooth wear is often used as a proxy for relative age in studies of living and fossil primates [Cuozzo et al., 2010]. Yet, there are many if not more variables that cannot easily be controlled for in the fossil record that, like those we describe here, affect the efficacy of assigning age to fossil specimens based on tooth wear [Morse et al., 2013; Sánchez-Villagra, 2010]. Our new data clearly show that relationships between wear-related tooth shape and age vary in a single primate population. Even at the

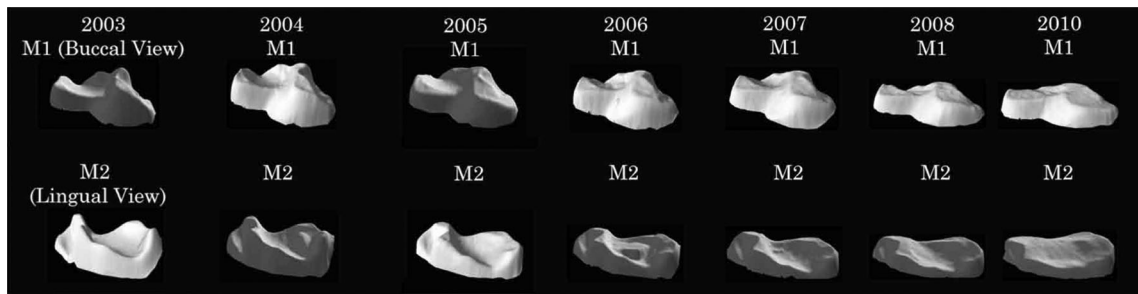


Fig. 4. Changes in M<sub>1</sub> and M<sub>2</sub> wear-related tooth shape in a female lemur (Orange 368, formerly Orange 168) from Beza Mahafaly from ages two (2003) through nine (2010).

young age of the individuals in this sample, microhabitat and sex differences in behavioral ecology contribute to this variation in wear-related tooth shape. The differences we illustrate herein may also predict what happens over time in older individuals, as we know that overall tooth wear does vary in lemurs greater than age 10 in this population [Cuzzo et al., 2010]. For example, lemur 168/368 shows a rather dramatic wear gradient from age 2–9 years (Fig. 4). Yet, in other lemurs of the same age, the degree of wear is nowhere near as dramatic [Cuzzo et al., 2010]. Our data show that differences in wear begin at an early age. This may in turn predict the wear trajectory of an individual later in life, which has potential impacts for life history, reproductive success, etc. Our continued, long-term work on this population of living primates, as they age, will provide further information for the interpretation of wear or wear-related shape changes and their relationships to age, habitat, and ecology in living and fossil species.

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## REFERENCES

Bunn JM, Ungar PS. 2009. Dental topography and diets of four old world monkey species. *American Journal of Primatology* 71:466–477.

- Cuzzo FP, Sauther ML. 2004. Tooth loss, survival, and resource use in wild ring-tailed lemurs (*Lemur catta*): implications for inferring conspecific care in fossil hominids. *Journal of Human Evolution* 46:623–631.
- Cuzzo FP, Sauther ML. 2006. Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): a function of feeding ecology, dental structure, and individual life history. *Journal of Human Evolution* 51:490–505.
- Cuzzo FP, Sauther ML. 2012. What is dental ecology? *American Journal of Physical Anthropology* 148:163–170.
- Cuzzo FP, Sauther ML, Gould L, et al. 2010. Variation in dental wear and tooth loss among known-aged, older ring-tailed lemurs (*Lemur catta*): a comparison between wild and captive individuals. *American Journal of Primatology* 72:1026–1037.
- Dennis JC, Ungar PS, Teaford MF, Glander KE. 2004. Dental topography and molar wear in *Alouatta palliata* from Costa Rica. *American Journal of Physical Anthropology* 125:152–161.
- Fish KD, Sauther ML, Loudon JE, Cuzzo FP. 2007. Coprophagy by wild ring-tailed lemurs (*Lemur catta*) in human-disturbed locations adjacent to the Beza Mahafaly Special Reserve, Madagascar. *American Journal of Primatology* 69:713–718.
- Galbany J, Altmann J, Pérez-Pérez A, Alberts SC. 2011. Age and individual foraging behavior predict tooth wear in Amboseli baboons. *American Journal of Physical Anthropology* 144:51–59.
- Gemmell A, Gould L. 2008. Microhabitat variation and its effects on dietary composition and intragroup feeding interactions between adult female *Lemur catta* during the dry season at Beza Mahafaly Special Reserve. *International Journal of Primatology* 29:1511–1533.
- Kay RF. 1975. The functional adaptations of primate molar teeth. *American Journal of Physical Anthropology* 43:195–216.
- Kay RF, Covert HH. 1983. True grit: a microwear experiment. *American Journal of Physical Anthropology* 61:33–38.
- Kay RF, Covert HH. 1984. Anatomy and behavior of extinct primates. In: Chivers DJ, Wood BA, Bilsborough A, editors. *Food acquisition and processing in primates*. New York: Plenum Press. p 479–508.
- King SJ, Arrigo-Nelson SJ, Pochron ST, et al. 2005. Dental senescence in a long-lived primate links infant survival to rainfall. *Proceedings of the National Academy of Sciences USA* 102:16579–16583.
- Klukkert ZS, Teaford MF, Ungar PS. 2012. A dental topographic analysis of chimpanzees. *American Journal of Physical Anthropology* 148:276–284.
- Lanyon JM, Sanson GD. 1986. Koala (*Phascolarctos cinereus*) dentition and nutrition. II. Implications of tooth wear in nutrition. *Journal of Zoology (London)* 209:169–181.
- Larsen RS, Sauther ML, Cuzzo FP. 2011a. Evaluation of modified techniques for immobilization of wild ring-tailed

- lemurs (*Lemur catta*). *Journal of Zoo and Wildlife Medicine* 42:623–633.
- Larsen RS, Moresco A, Sauther ML, Cuzzo FP. 2011b. Field anesthesia of wild ring-tailed lemurs (*Lemur catta*) using Tiletamine-Zolazepam, Medetomidine, and Butorphanol. *Journal of Zoo and Wildlife Medicine* 42:75–87.
- Logan M, Sanson GD. 2002a. The association of tooth wear with sociality of free-ranging male koalas (*Phascolarctos cinereus* Goldfuss). *Australian Journal of Zoology* 50:621–626.
- Logan M, Sanson GD. 2002b. The effects of tooth wear on the activity pattern of freeranging koalas (*Phascolarctos cinereus* Goldfuss). *Australian Journal of Zoology* 50:281–292.
- Looney SW, Stanley WB. 1989. Exploratory repeated measures analysis for two or more groups—review and update. *American Statistician* 43:220–225.
- Lucas PW. 2004. Dental functional morphology: how teeth work. Cambridge: Cambridge University Press. p 355.
- Lucas PW, Omar R, Al-Fadhalah K, et al. 2013. Mechanisms and causes of wear in tooth enamel: implications for hominin diets. *Journal of the Royal Society Interface* 10:20120923.
- M'Kirera F, Ungar PS. 2003. Occlusal relief changes with molar wear in *Pan troglodytes troglodytes* and *Gorilla gorilla gorilla*. *American Journal of Primatology* 60:34–41.
- Meldrum DJ, Kay RF. 1997. *Nucifraga rubicae*, a new pitheciin seed predator from the Miocene of Colombia. *American Journal of Physical Anthropology* 102:407–428.
- Millette JB, Sauther ML, Cuzzo FP. 2009. Behavioral responses to tooth loss in wild ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly Special Reserve, Madagascar. *American Journal of Physical Anthropology* 140:120–134.
- Millette JB, Sauther ML, Cuzzo FP, Ness JL. 2012. The impact of dental impairment on ring-tailed lemur food processing performance. *American Journal of Physical Anthropology* 148:238–248.
- Morse PE, Daegling DJ, McGraw WS, Pampush JD. 2013. Dental wear among cercopithecoid monkeys of the Taï Forest, Côte d'Ivoire. *American Journal of Physical Anthropology* 150:55–665.
- O'Mara MT. 2012. Development of feeding in ring-tailed lemurs [dissertation]. Tempe (AZ): Arizona State University. 262 p. Available from University Microfilms, Ann Arbor, MI, Dissertation Order Number 3505653
- Pampush JD, Duque AC, Burrows BR, et al. 2013. Homoplasy and thick enamel in primates. *Journal of Human Evolution* 64:216–224.
- Pereira ME. 1991. Asynchrony within estrous synchrony among ringtailed lemurs (Primates: Lemnidae). *Physiology and Behavior* 49:47–52.
- Phillips-Conroy JE, Bergman T, Jolly CJ. 2001. Quantitative assessment of occlusal wear and age estimation in Ethiopian and Tanzanian baboons. In: Jolly CJ, Whitehead P, editors. *Old world monkeys*. Cambridge: Cambridge University Press. p 321–340.
- Quinn G, Keough M. 2002. Experimental design and data analysis for biologists. New York: Cambridge University Press. p 556.
- Romero A, Galbany J, De Juan J, Pérez-Pérez A. 2012. Brief communication: short- and long-term in vivo human buccal-dental microwear turnover. *American Journal of Physical Anthropology* 148:467–472.
- Rosenberger AL, Kinzey WG. 1976. Functional patterns of molar occlusion in platyrrhine primates. *American Journal of Physical Anthropology* 45:281–297.
- Sánchez-Villagra MR. 2010. Developmental palaeontology in synapsids: the fossil record of ontogeny in mammals and their closest relatives. *Proceedings of the Royal Society B: Biological Sciences* 277:1139–1147.
- Sapolsky RM, Share LJ. 1998. Darting terrestrial primates in the wild: a primer. *American Journal of Primatology* 44: 155–167.
- Sauther ML. 1991. Reproductive behavior of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *American Journal of Physical Anthropology* 84:463–477.
- Sauther ML. 1992. Effect of reproductive state, social rank and group size on resource use among free-ranging ring-tailed lemurs (*Lemur catta*) of Madagascar [dissertation]. St. Louis (MO): Washington University. 315 p. Available from University Microfilms, Ann Arbor, MI, Dissertation Order Number 9234333.
- Sauther ML. 1994. Changes in the use of wild plant foods in free-ranging ring-tailed lemurs during lactation and pregnancy: some implications for hominid foraging strategies. In: Etkin NL, editor. *Eating on the wild side: the pharmacologic, ecologic, and social implications of using noncultigens*. Tucson: University of Arizona Press. p 240–246.
- Sauther ML. 1998. The interplay of phenology and reproduction in ring-tailed lemurs: implications for ring-tailed lemur conservation. *Folia Primatologica* 69(Suppl 1):309–320.
- Sauther ML. 2002. Group size effects on predation sensitive foraging in wild ring-tailed lemurs (*Lemur catta*). In: Miller LE, editor. *Eat or be eaten: predator sensitive foraging among primates*. Cambridge: Cambridge University Press. p 107–125.
- Sauther ML, Cuzzo FP. 2009. The impact of fallback foods on wild ring-tailed lemur biology: a comparison of intact and anthropogenically disturbed habitats. *American Journal of Physical Anthropology* 140:671–686.
- Sauther ML, Sussman RW. 1993. A new interpretation of the social organization and mating system of the ringtailed lemur (*Lemur catta*). In: Kappeler PM, Ganzhorn JU, editors. *Lemur social systems and their ecological basis*. New York: Plenum Press. p 111–121.
- Sauther ML, Sussman RW, Cuzzo F. 2002. Dental and general health in a population of wild ring-tailed lemurs: a new life history approach. *American Journal of Physical Anthropology* 117:122–132.
- Sauther ML, Sussman RW, Gould L. 1999. The socioecology of the ring-tailed lemur: thirty-five years of research. *Evolutionary Anthropology* 8:120–132.
- Sauther ML, Fish K, Cuzzo FP, et al. 2006. Patterns of health, disease and behavior among wild ring-tailed lemurs (*Lemur catta*): effects of habitat and sex. In: Jolly A, Sussman RW, Koyama N, Rasmimanana H, editors. *Ring-tailed lemur biology*. New York: Springer. p 313–331.
- Seligsohn D, Szalay FS. 1978. Relationship between natural selection and dental morphology: tooth function and diet in *Lepilemur* and *Haplemur*. In: Butler PM, Joysey KA, editors. *Development, function and evolution of teeth*. New York: Academic Press. p 289–307.
- Sokal RR, Rohlf FJ. 1995. *Biometry: the principles and practice of statistics in biological research*. 3rd edition. New York: W.H. Freeman. p 880.
- Sussman RW. 1991. Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. *American Journal of Physical Anthropology* 84:43–58.
- Sussman RW, Rakotozafy A. 1994. Plant diversity and structural analysis of a tropical dry forest in southwestern Madagascar. *Biotropica* 26:241–254.
- Sussman RW, Richard AF, Ratsirarson J, et al. 2012. Beza Mahafaly Special Reserve: a research site in Southwestern Madagascar. In: Kappeler P, Watts D, editors. *Long term field studies of primates*. New York: Springer. p 45–66.
- Teaford MF. 1983. The morphology and wear of the lingual notch in macaques and langurs. *American Journal of Physical Anthropology* 60:7–14.
- Ungar P. 2005. Reproductive fitness and tooth wear: milking as much as possible out of dental topographic analysis. *Proceedings of the National Academy of Science USA* 102: 16533–16534.

- Ungar PS. 2010. BT Mammal teeth: origin, evolution, and diversity. Baltimore: Johns Hopkins University Press. p 304.
- Ungar PS, M'Kirera F. 2003. A solution to the worn tooth conundrum in primate functional anatomy. *Proceedings of the National Academy of Science USA* 100:3874–3877.
- Ungar PS, Williamson M. 2000. Exploring the effects of tooth wear on functional morphology: a preliminary study using dental topographic analysis. *Paleontologica Electronica* 3:18.
- Ungar PS, Teaford MF, Glander KE, Pastor RF. 1995. Dust accumulation in the canopy: a potential cause of dental microwear in primates. *American Journal of Physical Anthropology* 97:93–99.
- Veiberg V, Mysterud A, Gaillard JM, et al. 2007. Bigger teeth for longer life? Longevity and molar height in two roe deer populations. *Biological Letters* 3:268–270.
- Vogel ER, van Woerden JT, Lucas PW, et al. 2008. Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. *Journal of Human Evolution* 55:60–74.
- Whitelaw DC. 2010. Ecological impacts of forest disturbance on ring-tailed lemurs (*Lemur catta*) in the Beza Mahafaly Special Reserve Region: implications for conservation in an altered landscape [dissertation]. Boulder (CO): University of Colorado-Boulder. 412 p. Available from University Microfilms, Ann Arbor, MI, Dissertation Order Number 3433354.
- Whitelaw DC, Sauter ML, Loudon J, Cuzzo F. 2005. Anthropogenic change in and around Beza-Mahafaly reserve: methodology and results. *American Journal of Physical Anthropology* 126(Suppl 40):222.
- Williams SH, Kay RF. 2001. A comparative test of adaptive explanations for hypsodonty in ungulates and rodents. *Journal of Mammalian Evolution* 8:207–229.
- Yamashita N. 2002. Diets of two lemur species in different microhabitats in Beza Mahafaly special reserve, Madagascar. *International Journal of Primatology* 23:1025–1051.
- Yamashita N, Cuzzo FP, Sauter ML. 2012. Interpreting food processing through dietary mechanical properties: a *Lemur catta* case study. *American Journal of Physical Anthropology* 148:205–214.
- Zuccotti LF, Williamson MD, Limp WF, Ungar PS. 1998. Modeling primate occlusal topography using geographic information systems technology. *American Journal of Physical Anthropology* 107:137–142.